Disentangling a complex genus: systematics, biogeography and bioactivity of the genus Phyllanthus L. and related genera of tribe Phyllantheae (Phyllanthaceae)

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CHAPTER 3

Subgeneric delimitation of the plant genus *Phyllanthus* (Phyllanthaceae)

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Chapter 3

Subgeneric delimitation of the plant genus Phyllanthus (Phyllanthaceae)

Short title: Subgeneric delimitation of *Phyllanthus*

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Abstract
Over two centuries of taxonomic studies on the species rich genus *Phyllanthus* have culminated in a broad and complicated classification with many subgenera and (sub)sections. Past taxonomic work has only focused on local revisions, mostly because of the size of the genus. In this study we aim to summarize most of the taxonomic work in a list containing the infrageneric delimitations of *Phyllanthus*. This work will serve as a reference, placing most currently recognized species in subgenera and if possible, in sections for further study. Here we recognize 880 species of Phyllanthus, classified in 18 subgenera, 70 sections and 14 subsections. A few taxonomic changes are necessary to reconcile published phylogenetic data with the current classification. Subsections *Callidisci* and *Odontadenii* are raised to sectional rank, while section *Eleutherogynium* and section *Physoglochidion* are reduced to subsections and *P. oxycarpus* is transferred to the genus *Glochidion*. A provisional key for the subgeneric classification of *Phyllanthus* is provided.

Key words: infrageneric taxonomy, pantropical, paraphyletic, Phyllanthaceae, Phyllanthus

Introduction
With almost 900 species, the mostly pantropical *Phyllanthus* L. is the largest genus in the family Phyllanthaceae (Govaerts et al. 2000). When considering all vegetative and reproductive organs, *Phyllanthus* is one of the most diverse groups in the Angiosperms (Webster 1956). This diversity is exemplified by the multitude of subgenera and (sub)sections defined within the genus. In the past, most of these

subgenera and some sections were treated at generic rank (Jussieu 1824, Baillon 1858), but were eventually all subsumed in a broad genus concept of *Phyllanthus* with numerous sections (Müller 1863, 1865, 1866). The last major changes to this concept at genus level have been the segregation of the genera *Glochidion* J.R.Forst. & G.Forst. (Kurz 1873) and *Margaritaria* L.f. (Webster 1957, 1979). The infrageneric structure of *Phyllanthus* was improved with the creation of several subgenera in a monographic work on the *Phyllanthus* species of the West Indies by Webster (1956, 1957, 1958). Subsequent revisionary work followed Webster's outline of subgenera and sections to illustrate the relations among groups within *Phyllanthus* (e.g. Bancilhon 1971; Webster & Airy Shaw 1971; Punt 1972; Airy Shaw 1975, 1980a; Brunel 1987; Rossignol et al. 1987; Santiago et al. 2006; Ralimanana & Hoffmann 2011, 2014; Ralimanana et al. 2013). Regional work on *Phyllanthus* (Merrill 1920, 1926; Pax & Hoffmann 1922; Beille 1925, 1927; Croizat 1942a, 1943b; Leandri 1958; Airy Shaw 1963, 1969, 1972, 1975, 1976, 1980a, 1980b, 1982; Webster 1986; Chantaranothai 2005; Silva & Sales 2006, 2008) and morphological studies (Punt 1967, 1972, 1973, 1980, 1986; Lobreau-Callen et al. 1988; Stuppy 1995; Chen et al. 2009; Jangid & Gupta 2016; Wu et al. 2016) extended the infrageneric groupings to create a working classification for most *Phyllanthus* species.

However, recent phylogenetic studies showed that several subgenera were polyphyletic and even *Phyllanthus* itself proved to be paraphyletic (Kathriarachchi et al. 2006). In the following taxonomic revisions some of the polyphyletic subgenera were divided in new monophyletic subgenera (Ralimanana & Hoffmann 2011, 2014a; Ralimanana *et al.* 2013), but discussion remained whether *Breynia* J.R.Forst. & G.Forst., *Glochidion* and *Sauropus* Blume should be subsumed into *Phyllanthus*. One solution is to subsume these genera in *Phyllanthus* to create a giant genus (Hoffmann et al. 2006, followed by Chakrabarty & Balakrishnan 2009b; Wagner & Lorence 2011; Kurosawa 2016) and the other is to split *Phyllanthus* into smaller, morphologically recognizable, monophyletic groups (Pruesapan et al. 2012; van Welzen et al. 2014a; Telford et al. 2016, followed by Chakrabarty & Balakrishnan 2012). A more exhaustive phylogenetic study with higher sampling presented the case to maintain *Breynia* (including *Sauropus*), *Synostemon* F.Muell. and *Glochidion* as monophyletic and morphologically recognizable genera (Pruesapan et al. 2008, 2012; van Welzen et al. 2014a), still leaving the rest of *Phyllanthus* in its current state, a paraphyletic genus. If *Phyllanthus* would be split, a larger phylogenetic study, which includes all subgenera and the majority of sections, is needed to prove which groups are monophyletic.

Phyllanthus is currently classified in about 18 subgenera with numerous sections by past revision work. The most notable revisions of *Phyllanthus* are those for the neotropics (Webster 2001b, 2002a, 2002b, 2004), Asia (Airy Shaw 1960, 1975, 1980, 1981; Webster & Airy Shaw 1971; Schmid 1991) and tropical Africa and Madagascar (Brunel 1987; Brunel & Roux 1975, 1976, 1977, 1981, 1984, 1985; Leandri 1958; Radcliffe-Smith 1974, 1996b; Ralimanana & Hoffmann 2011,

2014, Ralimanana et al. 2013). There is some discussion regarding the validity as publication of Brunel's thesis (1987). The thesis covers a large amount of work on the *Phyllanthus* species of Madagascar and Africa with many notes on subgenera and sections. Because it is a thesis, this work was treated as not validly published based on article 32 of the International Code of Botanical Nomenclature (McNeill et al. 2012) by Kathriarachchi et al. (2006). However, the thesis contains the name of a printing company and numbered copies have been distributed to several institutes, which is all in agreement with article 30.8, making it a validly published book. As such it is used in this publication. Several of the decisions in Brunel's thesis were accepted in recent revisions of *Phyllanthus* in Madagascar (Ralimanana & Hoffmann 2011, 2014, Ralimanana et al. 2013).
The checklist by Govaerts et al. (2000) is often used to estimate the number of species within *Phyllanthus,* but it does not contain an infrageneric division. An attempted synopsis of all the subgenera and sections was published by Kathriarachchi et al. (2006). However, only the species included in the phylogenetic study were mentioned and a complete taxonomic treatment of the genus is still wanting. We hope that this list may serve as a framework for future studies. If *Phyllanthus* should ever be split into various genera, this list can serve as a recommendation for the species to include.

Methods
In this study, we record 881 species, which are divided into 18 subgenera, 69 sections and 15 subsections (Appendix 3-1). Govaerts et al. (2000) recorded 833 species and the difference is mainly caused by the acceptance of Brunel (1987) and the addition of newly published species after their work. Based on a combination of morphological descriptions, classifications in literature and published phylogenetic work (e.g., Samuel et al. 2005; Kathriarachchi et al. 2006; Pruesapan et al. 2008, 2012; Manissorn et al. 2010; Challen et al. 2011; Luo et al. 2011a), we propose the current list for the subgeneric classification of *Phyllanthus*, in which we assign as many species as possible to subgenera and sections. Some placements are adopted from and are now validly published from Webster's unfinished manuscripts, which are available online (http://herbarium.ucdavis.edu/webster_manuscripts.html). For those species that were unplaced, we studied the distribution and morphological descriptions (mainly branching type and the morphology of the staminate flower), which allowed us to place them at least in subgenera. A synoptic key is provided by which most species can be placed in the appropriate subgenera and/or sections. However, sections and the species included have often not been the subject of recent taxonomic revisions or are based solely on palynological differences. This complicates the creation of a key that can accommodate all species of *Phyllanthus*. The most important literature is cited after each species, which either provides a direct placement or a morphological description. Hybrid species and infraspecific taxa were not included. Some combinations, partly required by changes in level, are

published here, but only to solve nomenclatural anomalies (e.g., subsections that cannot be classified anymore in a section due to splitting of sections and changes in the taxonomic level of the taxa).

Taxonomy listing of *Phyllanthus*

We could assign 837 of the 880 species to a particular subgenus or (sub)section (Appendix 3-2), with some only listed as formerly in subgenus *Isocladus* or the synonymized section *Paraphyllanthus* Müll.Arg. One species of subgenus *Isocladus* G.L.Webster, *P. maderasatensis* L., was designated as the lectotype of the whole genus *Phyllanthus* by Ralimanana & Hoffmann (2011). However, *Phyllanthus niruri* L. was already designated as the lectotype of the genus *Phyllanthus* by Small (1913) and later independently confirmed by Webster (1956). Unfortunately, the remaining 43 species could not be assigned due to either incomplete descriptions, destroyed type specimens, or lack of collections. We have opted to place these species *incertae sedis* as their true relations need further detailed study.

The classification of several subgenera from Webster's original monographs (1956, 1957, 1958) has changed drastically. Subsequent palynological (e.g., Punt 1967, 1972, 1973, 1980, 1986; Lobreau-Callen et al. 1988) and phylogenetic studies (Kathriarachchi et al. 2006) have led to many new combinations and necessary transfers, some of which are discussed below.

Subgenus *Isocladus* Webster was created to include about 60 species with non-phyllanthoid branching (leaves on main stem not reduced to scales and lateral axes not deciduous) and consisted of originally four sections, *Loxopodium* G.L.Webster, *Anisolobium* Müll.Arg., *Macraea* (Wight) Baill. and *Paraphyllanthus* Müll.Arg. (Webster 1956). However, subsequent studies (Brunel 1987, Webster 2002b) have reduced the size of this subgenus considerably. The sections *Macraea* and *Ceramanthus* (Hassk.) Baill. (the latter with section *Anisolobium* merged with it; Punt 1972) were raised to subgeneric level by Brunel (1987). Section *Loxopodium* has been transferred to subgenus *Phyllanthus* on the basis of pollen characteristics and section *Paraphyllanthus* was placed in the synonymy of section *Isocladus* (Brunel 1987). Webster did create a new section in subgenus *Isocladus*, *Antipodanthus* G.L.Webster, which contained several neotropical and Australian species (Webster 2002a), but the Australian species appear to be better placed in section *Lysiandra* (F. Muell.) G.L.Webster of subgenus *Phyllanthus* (Bouman, unpublished data). Phylogenetic studies have confirmed the distinctness of subgenera *Macraea* and *Ceramanthus* from *Loxopodium* (Kathriararchchi et al. 2006). For section *Antipodanthus*, only one Australian species, *P. calycinus* Labill., and no neotropical species were included in the phylogeny by Kathriararchchi et al. (2006), in which the group appeared to be distinct from subgenus *Isocladus*. However, to elucidate the relationship between sections *Antipodanthus* and *Lysiandra* it is necessary to include more species in a phylogenetic study. Therefore section *Antipodanthus* is here maintained with no formal subgeneric placement.

Ralimanana & Hoffmann (2011) made the remainder of subgenus *Isocladus* (including former section *Paraphyllanthus*) monotypic, to only include *P. maderaspatensis* L., leaving some species unplaced and in need of revision.

All small shrubs and herbaceous *Phyllanthus* species were originally placed in subgenus *Phyllanthus*. The subgenus was shown to be polyphyletic (Kathriarachchi et al. 2006) and several subgenera are now recognized separately: subgenus *Swartziani* (G.L.Webster) Ralim. & Petra Hoffm., containing the neotropical herbaceous species of subsection *Swartziani*; subgenus *Afroswartziani* Ralim. & Petra Hoffm., comprising the palaeotropical species of former subsection *Swartziani* (largely comparable with section *Anthophyllus* Jean F.Brunel (Brunel 1987)), subgenus *Tenellanthus* Jean F.Brunel and subgenus *Phyllanthus.* Subgenus *Phyllanthus* now only contains sections *Almadenses* G.L.Webster, *Choretropsis* Müll. Arg., *Loxopodium* G.L.Webster, *Lysiandra*, *Phyllanthus* and *Salviniopsis* Holm-Niels. ex Jean F.Brunel. Section *Praephyllanthus* Jean F.Brunel was found to be closely related to the species of subgenus *Afroswartziani* (Kathriarachchi et al. 2006) and is transferred here to subgenus *Afroswartziani*. The type of section *Anthophyllus* was placed in subgenus *Swartziani*, but all other palaeotropical species, including subsections *Callidisci* Jean F.Brunel, *Fluitantoides* Jean F.Brunel and *Odontadenii* Jean F.Brunel & Roux (here raised to section level) are better placed in subgenus *Afroswartziani*. These two subgenera are closely related (see Kathriarachchi et al. 2006) and mostly distinguished by the inflorescences (unisexual in *Afroswartziani*, bisexual in *Swartziani*) (Ralimanana et al. 2013). The species in sections *Odontadenii, Fluitantoides* and *Callidisci* have unisexual inflorescences and are tentatively placed in subgenus *Afroswartziani*.

Subgenus *Kirganelia* (A.Juss.) Kurz is polyphyletic (Kathirarachchi et al. 2006) and currently consists of eight sections: *Anisonema* (A.Juss.) Griseb., *Brazzeani* Jean F.Brunel & Roux, *Chorisandra* (Wight) Müll.Arg., *Cicca* (L.) Müll. Arg., *Hemicicca* (Bail.) Müll.Arg., *Omphacodopsis* Jean F.Brunel, *Polyanthi* Jean F.Brunel and *Pseudomenarda* Müll.Arg. As noted by Ralimanana & Hoffmann (2011), the type species for subgenus *Kirganelia* is *P. casticum* P.Willemet, but *P. reticulatus* Poir. is the type species for the type section *Anisonema*. Some African and Madagascan species, originally attributed to this subgenus, were shown to be phylogenetically separate and placed in subgenus *Anesonemoides* (Jean F.Brunel) Ralim. & Petra Hoffm. (Ralimanana & Hoffmann 2014). Subgenus *Anesonemoides* differs from subgenus *Kirganelia* in fruit morphology (dehiscent in subgenus *Anesonemoides* versus baccate in subgenus *Kirganelia*), a lack of brachyblasts in some species of subgenus *Anesonemoides*, pollen with colpi bordered by parallel muri and the androecium (free or centrally fused stamens in subgenus *Anesonemoides* versus two sets of stamens (one fused, one free) in subgenus *Kirganelia*) (Ralimanana & Hoffmann 2014). Subgenus *Kirganelia* sections *Cicca* and *Chorisandra* were also shown to be in a clade separate from section *Anisonema* (Kathriarachchi et al. 2006), but no nomenclatural changes have yet been published.

The sections *Omphacodopsis*, *Polyanthi* and *Brazzeani* have not yet been included in any phylogenetic studies. Section *Brazzeani* was originally placed in subgenus *Conami* (Aubl.) G.L.Webster based on pollen characters (Brunel & Roux 1977), but these seem to have arisen through convergence and *Brazzeani* is better placed in subgenus *Kirganelia* (Meeuwis & Punt 1983). The stamen in the staminate flowers of section *Brazzeanii* are arranged in two sets, similarly to subgenus *Kirganelia* section *Anisonema*. Though still used in Kathriarachchi et al. (2006) and Ralimanana & Hoffmann (2011), section *Floribundi* Pax & K.Hoffm. was reorganized by Brunel (1987) into two new sections *Polyanthi* and *Omphacodopsis*, while the type species of section *Floribundi* (*P. muellerianus* (Kuntze) Exell) was transferred to section *Anisonema*, and the two sections were combined. Sections *Polyanthi* and *Omphacodopsis*, though distinguished by pollen and fruit (in)dehiscence by Brunel (1987), can possibly be combined (see Breteler 2012). The staminate flowers of these sections are similar to species in subgenus *Anesonemoides*, but the indehiscent fruit is more like subgenus *Kirganelia* section *Anisonema* or *Cicca*.

Subgenus *Emblica*, sections *Microglochidion* (Müll.Arg.) Müll.Arg., *Pityrocladus* G.L.Webster (subg. *Emblica*) and subgenus *Cyclanthera* G.L.Webster were not yet included in any phylogenetic research and their relationships within *Phyllanthus* are not well known. Webster chose to include section *Microglochidion* and *Pityrocladus* in the Asiatic subgenus *Emblica* on account of their similarity in pollen (Webster 2002b; Webster & Carpenter 2002, 2008). A possible relationship between subgenus *Cyclanthera* and subgenus *Xylophylla* was suggested by Brunel (1987), but not incorporated in the latest revision by Webster (2002b).

Kathriarachchi et al. (2006) listed several sections as "not assigned to subgenus", which are either already placed by other authors, placed here, or treated as synonyms. Sections *Bivia* Jean F.Brunel & Jacq.Roux, *Ceramanthus* (Hassk.) Baill. and *Cluytopsis* Müll.Arg. are all placed in subgenus *Ceramanthus* (Punt 1972; Brunel & Roux 1985; Brunel 1987). Section *Nymphanthus* (Lour.) Müll.Arg. has often been treated in subgenus *Phyllanthus* (Li 1987a), but is placed here in subgenus *Eriococcus* (Hassk.) Croizat & Metcalf based on its pollen morphology (see Webster 1958; Brunel 1987; Webster & Carpenter 2008). Species of subgenus *Eriococcus* occur in Asia and Australia and are characterized by the staminate flower with four sepals and two or four stamens. Section *Physoglochidion* Müll. Arg is placed here as a subsection under section *Gomphidium* Baill. based on the treatment of Schmid (1991), which is discussed below. Subgenus *Gomphidium* is a diverse group, with its main centres of diversity in New Guinea and New Caledonia. The monotypic section *Hemicicca* Baill. is here placed in subgenus *Kirganelia* based on its similarity in pollen (see Brunel 1987) and baccate fruits. The remaining previously un-assigned sections are here treated as synonyms: section *Heteroglochidion* Müll.Arg. is a synonym of subsection *Eleutherogynium* (Müll.Arg.) G.L.Webster ex R.W.Bouman (see below for new combination based on Webster 1986); sections *Meiandroglochidion* S.Moore and *Polyandroglochidion* S. Moore are

synonyms of section *Adenoglochidion* (Müll.Arg.) Müll.Arg. (Schmid 1991); section *Pentaglochidion* Müll.Arg.is a homeotypic synonym of section *Leptonema* Baill. (see Baillon 1862b; Müller 1863). The type species of section *Hedycarpidium* Müll. Arg. has been re-identified as *Baccaurea javanica* (Blume) Müll.Arg (see Müll.Arg. 1866; Haegens 2000) and even though the name is sometimes still used (Thin 2007), it is invalid and the other species assigned to this section need to be re-evaluated. A small number of *Phyllanthus* species from Vietnam was placed in subgenus *Eriococcus* subsection *Integra* Thin (see Thin 2007), which is not included in our list. No description was provided and it is quite possibly a synonym of subgenus *Eriococcus* subsection *Spiciferens* Jean F.Brunel as they include some of the same species, but we were not able to see the original publication.

Some nomenclatural issues are still present within *Phyllanthus*, particularly when looking at the names of subdivisions of certain subgenera. Recommendation 22A of the International Code of Nomenclature (McNeill et al. 2012) states that if there are no problems any subdivision of a subgenus that bears the type, should be given the same epithet. However in a few subgenera, this is currently not the case (Webster 1960). The type section of subgenus *Conami* is section *Nothoclema* G.L.Webster and the type section of subgenus *Kirganelia* is *Anisonema*. In subgenus *Kirganelia* section *Cicca*, the type species, *P. acidus* (L.) Skeels, is in subsection *Cheramela* Kuntze (Webster 2001b).

Taxonomic changes

Phyllanthus subgenus **Afroswartziani** Ralim. & Petra Hoffm. section **Callidisci** (Jean F.Brunel) R.W.Bouman, stat nov.—*Phyllanthus* subsect. *Callidisci* Jean F.Brunel, Gen. *Phyllanthus* Afr. Intertrop. Madag. (1987) 334. — Type: *Phyllanthus callidiscus* Jean F.Brunel

Note — Species of section *Callidisci* were originally placed by Brunel (1987) in subgenus *Phyllanthus* section *Anthophyllus* together with other palaeotropical subsections and recognized by the fringed disc in the pistillate flowers. As this group has recently been shown to be polyphyletic (Kathriarachchi et al. 2006) and after revision were split into a few new subgenera (Ralimanana et al. 2013), it seems necessary also to transfer Brunel's subsections. All other palaeotropical species of subgenus *Phyllanthus* were placed in subgenus *Afroswartziani* and were distinguished from the neotropical subgenus *Swartziani* by their unisexual inflorescences (Ralimanana et al. 2013). This is in agreement with species of subsection *Callidisci*, which is transferred here and raised to sectional level to accommodate the separation from section *Anthophyllus*.

Phyllanthus subgenus **Afroswartziani** Ralim. & Petra Hoffm. section **Odontadenii** (Jean F.Brunel & Jacq.Roux) R.W.Bouman, stat nov.—*Phyllanthus* subsect. Odontadenii Jean F.Brunel & Jacq.Roux, Willdenowia 11 (1981) 70; Brunel, Gen. *Phyllanthus* Afr. Intertrop. Madag. (1987) 339. — Type: *Phyllanthus odontadensis*

Müll.Arg.
Note — Species in the palaeotropical section *Odontadenii* also have unisexual inflorescences and are therefore more suited to be placed in subgenus *Afroswartziani* then the neotropical subgenus *Swartziani*. The species are distingusihed form other sections by their winged plagiotropic branchlets (Brunel & Roux 1981).

Phyllanthus subgenus **Gomphidium** (Baill.) G.L.Webster section **Adenoglochidion** (Müll.Arg.) Müll.Arg. subsection **Eleutherogynium** (Müll.Arg.) G.L.Webster ex R.W.Bouman, stat nov. — *Phyllanthus* sect. *Eleutherogynium* Müll. Arg., Linnaea 32 (1863) 4, 14. — Type: *Phyllanthus loranthoides* Baill.
Glochidion sect. *Chorizogynium* Müll.Arg., Linnaea 32 (1863) 58, 59. — Lectotype (designated by Webster 1986): *Phyllanthus macrochorion* Baill.
Phyllanthus sect. *Heteroglochidion* Müll.Arg. in A.DC., Prodr. 15,2 (1866) 319. — Type: *Phyllanthus baladensis* Baill.
Phyllanthus sect. *Scleroglochidion* Müll.Arg. in A.DC., Prodr. 15,2 (1866) 317. — Type: *Phyllanthus myrianthus* Müll.Arg.
Note — Section *Scleroglochidion*. was previously placed in synonymy by Webster (1986) who expanded the description of *Eleuterhogynium* to include also *Phyllanthus* species with 3 free filaments. Section *Heteroglochidion* was defined by Müller on its biseriate sepals, which is a common character for subgenus *Gomphidium*. All of these sections are characterized by a rudimentary to absent nectar disc (see Müll.Arg. 1866). Lobreau-Callen et al. (1988) in a palynological study, showed that the pollen of these groups showed a continuous variation in pollen characters and were difficult to differentiate. The lack of distinguishing floral and vegetative characters and the overlap in palynological characters leads us to the decision to combine the above sections in one subsection *Eleutherogynium*, with as main character the absent nectar disc to distinguish it from other species within section *Adenoglochidion*.

Phyllanthus subgenus **Gomphidium** (Baill.) G.L.Webster section **Gomphidium Baill.** subsection **Physoglochidion** (Müll.Arg.) R.W.Bouman, stat nov.— *Glochidion* sect. *Physoglochidion* Müll.Arg., Linnaea 32 (1863) 58.— *Phyllanthus* sect. *Physoglochidion* (Müll.Arg.) Müll.Arg., Prodr. 15,2 (1866) 318. — Type: *Phyllanthus faguetii* Baill.
Phyllanthus sect. *Phyllocalyx* Baill., Adansonia 2 (1862b) 236 (nom. illeg., non *Phyllocalyx* A.Richert, 1847)— *Glochidion* sect. *Physoglochidion* Müll.Arg., Linnaea 32 (1863) 58, 71. — Lectotype (designated here by R.W.Bouman, but see Webster (2001) manuscript synopsis of *Gomphidium*): *Phyllanthus faguetii* Baill.
Note — *Phyllanthus* section *Physoglochidion* (Müll.Arg.) Müll.Arg. is characterized by 3 free stamens, 6 sepals in two whorls and a calyx that becomes saccate in fruit. Apart from the saccate calyx, these characters also occur in section *Gomphidium*

and within section *Physoglochidion* and the saccate calyx shows a continuous variation between species (Lobreau-Callen et al. 1988). Since these groups can also not be distinguished on palynological data we opt to reduce section *Physoglochidion* to a subsection level and place it with section *Gomphidium*.

Transfer of *Phyllanthus oxycarpus* to *Glochidion*:
Glochidion oxycarpum (Müll.Arg.) R.W.Bouman, comb. nov.
Phyllanthus oxycarpus Müll.Arg., Prodr. 15,2 (1866) 1270. – *Diasperus oxycarpus* (Müll.Arg.) Kuntze, Rev. Gen. Pl. 2 (1891) 600. – Type: *Teijsmann* s.n. (holotype GDC), Indonesia, Sumatra.
Note — In his treatment of the genus *Phyllanthus* for de Candolle, Müller (1866) reduced the genus *Glochidion* to a few sections within *Phyllanthus*. *Phyllanthus oxycarpus* Müll.Arg. was first described by Müller (1866) and placed in section *Euglochidion* Müll.Arg. as it closely resembled *P. subscandens* (Zoll. & Moritzi) Müll. Arg. (a synonym of *G. zeylanicum* (Gaertn.) A.Juss.). Other species first published in section *Euglochidion* by Müll.Arg. were all transferred to the genus by other authors (e.g., Boerlage 1900; Koorders & Valeton 1910), but we were unable to find a transfer for *G. oxycarpum*. The description lists no nectar disc, a 5-6-locular ovary with columnar style, which are all typical features for the genus *Glochidion* and therefore this species is transferred here.

Key to the subgenera and (sub) sections of *Phyllanthus*
A provisional key is here provided based on characters mentioned in the literature. A key for full identification purposes, using morphology only (not pollen) is difficult due to the absence of recent complete treatments for several groups and the fact that some characters have evolved multiple times within *Phyllanthus*. The key is not completely dichotomous (trichotomous questions are marked with *) Authors of the various subgenera, sections and subsections are listed in Appendix 3-1 and all species within a particular group are listed in Appendix 3-2.

1. Branching non-phyllanthoid (laminate leaves and flowers on all axes, branchlets not deciduous).....2
1. Branching phyllanthoid (leaves on main stem reduced to scales, cataphylls, laminate leaves and flowers on lateral axes, lateral branchlets deciduous) or sub-phyllanthoid (leaves at base of branchlets not reduced to scales (often in juveniles), lateral branchlets deciduous)..... 15

2. Aquatic herbs..... Subgenus *Phyllanthus* section *Salviniopsis* (Americas)
2. Herbs, shrubs or trees, but not aquatic 3

3. Palm-like (monocaul) shrubs to trees; stigma petaloid..... ..... Subgenus *Xylophylla* section *Asterandra* (South America)

3. Herbs, shrubs to small trees, rarely climbers; stigmas variously bifid to multifid, not petaloid 4

4. Leaves on all axes spirally arranged 5
4. Leaves on all axes distichous 9

5. Sepals 4 in staminate flowers, 6 in pistillate flowers; staminate disc entire, H-shaped around filaments; stamens 2, filaments free ..... Subgenus *Swartziani* section *Reverchonia* (North America)
5. Sepals 5–6 sepals in both sexes; staminate disc segmented; stamens 3 or 5, filaments free or connate 6

6. Sepals 5; stamens 5, filaments free ..... Subgenus *Kirganelia* section *Pseudomenarda* (Africa)
6. Sepals 5–6 sepals; stamens usually 3, filaments connate (free in *P. rosmarinifolius* Müll.Arg.) 7

7. Inflorescences axillary cymules with 1–4 flowers; pistillate disc consisting of free glands ..... Subgenus *Isocladus* (Africa and Asia, introduced in North America)
7. Inflorescences axillary cymules or thyrses; pistillate disc entire 8

8. Inflorescences axillary glomerules; pollen 3–4-colporate, subglobose ..... Section *Antipodanthus* incertae sedis (South America & Australia?)
8. Inflorescences axillary glomerules or thyrses (sometimes paniculate at end of branch); pollen areolate ..... Subgenus *Xylophylla* section *Elutanthos* (Central and South America)

9. Staminate disc segmented, pistillate disc entire or segmented; filaments free 10
9. Staminate disc segmented, or entire and urceolate, pistillate disc often massive and urceolate; filaments connate — pollen with macroreticulate exine ..... 12 (subgenus *Ceramanthus*)

10. Anthers dehiscing with horizontal slits; pollen 4-colporate ..... Subgenus *Phyllanthus* section *Loxopodium* (Americas)
10. Anthers often deflexed, but dehiscing with vertical slits; pollen clypeate or perisyncolporate 11

11. Leaves distichous; pollen clypeate; seeds verrucate or smooth ..... Subgenus *Macraea* (Africa, Asia, Australia and Pacific)
11. Leaves spiral at basal nodes, distichous at upper nodes; pollen grains

perisyncolporate with median pores, colpi bordered by parallel muri; seeds smooth or striate ..... Subgenus *Betsileani* (Madagascar)

12. Staminate flowers with sepals 4 (6 in pistillate ones); staminate disc consisting of 4 massive segments; stamens 2, filaments connate and thecae on an enlarged connective — pollen stephanoporate ..... Subgenus *Ceramanthus* section *Bivia* (Africa)
12. Sepals 6 in both sexes; staminate disc entire or 6 segments; stamens 3 with connate filaments, thecae not on an enlarged connective 13

13. Staminate disc entire and cup-shaped ..... Subgenus *Ceramanthus* section *Ceramanthus* (Asia)
13. Staminate disc segmented or only slightly fused into a ring 14

14. Sepals in two dimorphic whorls; staminate disc segmented; pollen peribrevicolporate ..... Subgenus *Ceramanthus* section *Anisolobium* (Africa and Asia)
14. Sepals in two equal whorls; staminate disc segmented to slightly fused into a ring; pollen pantoporate..... Subgenus *Ceramanthus* section *Cluytopsis* (Asia)

15. Branching sub-phyllanthoid 16
15. Branching phyllanthoid (sometimes sub-phyllanthoid in very young plants, check mature plants) 20

16. Branchlets short, with only 5–10 leaves (Webster 2001b); staminate disc entire ..... Subgenus *Xylophylla* section *Brachycladus* (South America and Central America)
16. Branchlet length variable, usually bearing more than 10 leaves; staminate disc segmented 17

17. Anther connective not enlarged; fruit an indehiscent capsule; seeds smooth with fleshy sarcotesta ..... Subgenus *Conami* section *Hylaeanthus* (South America and West Indies)
17. Anther connective variable, often enlarged; fruit a dehiscent capsule; seeds ornamented, without a fleshy sarcotesta 18

18. Filaments connate, stamens mostly 3 .....26 (subgenus *Afroswartziani*)
18. Filaments free (filaments connate in *P. allemii* G.L.Webster and *P. fastigiatus* Mart ex Müll.Arg., but then only 2 stamens) 19

19. Anther connective often enlarged, thecae not appearing as stipitate; seeds

scalariform with slight transverse striations or smooth..... .Subgenus *Phyllanthus* section *Lysiandra* (Australia and Central America(?))

19. Anther connective variable, sometimes deeply emarginate with the two thecae appearing to be stipitate; seeds striate or linearly verrucate..... .....Subgenus *Phyllanthus* section *Phyllanthus* subsection *Clausseniani* (South America)

20. Herbs or subshrubs 21
20. Shrubs to trees, rarely climbers 36

21. Herbs; each branchlet bearing just one pair of (sub)opposite leaves and terminating in a raceme; anther connective enlarged..... .....Subgenus *Phyllanthus* section *Phyllanthus* subsection *Almadanses* (South America)
21. Herbs or subshrubs; branchlet with more than 2 alternate leaves and flowers in leaf axils; anther connective (not) enlarged 22

22. Flowers 5-merous; stamens 5, filaments free (except 3 stamens in *P. cocumbiensis* Jean F.Brunel) — pollen subglobose, 3–4-colporate ....23 (Subgenus *Tenellanthus* pantropical, but origin Africa)
22. Flowers 5–6-merous; stamens 2–3, filaments free or connate..... 24

23*. Shrubs or hemicryptophytes; stamens 5, filaments basally united; pollen 3-colporate, with macroreticulate exine. Seeds with fine punctuation..... ..... Subgenus *Tenellanthus* section *Loandani* (Africa)
23*. Herbs; stamens 5 (3 in *P. cocumbiensis*), filaments connate or free; pollen 3-colporate, with tectate, microperforate exine ....Subgenus *Tenellanthus* section *Pentandra*(Africa)
23*. Herbs or subshrubs; stamens 5, filaments completely free; pollen 4-colporate with sponge-like exine..... ..Subgenus *Tenellanthus* section *Tenellanthus* (pantropical, but origin Africa)

24. Inflorescences unisexual..... 25
24. Inflorescences bisexual 35

25. Cataphyllary stipules (unilaterally) auriculate 26
25. Cataphyllary stipules not auriculate 32

26. Leaf base symmetric; plagiotropic branches carinate (winged) (Brunel & Roux 1981). Pollen exine tectate; seeds with longitudinal striae or smooth..... ..... Subgenus *Afroswartziani* section *Odontadenii* (Africa)
26. Leaf base asymmetric; plagiotropic branches not carinate..... 27

27. Pistillate disc entire with delicate fringes ..... Subgenus *Afroswartziani* section *Callidisci* (Africa)
27. Pistillate disc entire, but not fringed 28

28. Sepals 5 in staminate flowers 29
28. Sepals 6 in staminate flowers 30

29. Cataphyllary stipules usually black and indurate; stamen 2–3, filaments partially or wholly connate, anthers sometimes deeply emarginate, dehiscing mostly horizontal; seeds longitudinally striate or banded, possibly with transverse striae. Pollen 3-colporate ..... Subgenus *Phyllanthus* section *Phyllanthus* subsection *Pentaphyllus* (West Indies)
29. Cataphyllary stipules thin and membranous, not indurate or black; stamen 3, filaments connate, anthers not emarginate, dehiscing horizontally to vertically; seeds longitudinally striate 30

30. Pistillate inflorescences on proximal position and staminate inflorescences on distal position of plagiotropic branchlets; seeds transversely striate — ovary often covered with tubercles ..... Subgenus *Emblica* section *Urinaria* (pantropical, but origin Asia)
30. Pistillate inflorescences on distal position and staminate inflorescences on proximal position of plagiotropic branchlets; seeds longitudinally striate .. 31 (Subgenus *Afroswartziani*)

31*. Pollen 3–4-colporate, exine bireticulate ..... Subgenus *Afroswartziani* section *Praephyllanthus* (Africa)
31*. Pollen 3-sulcate, exine macroreticulate. Often found in water ..... Subgenus *Afroswartziani* section *Fluitantoides* (Africa)
31*. Pollen perihexabrevisulcate, exine macro-rugulose (Brunel 1987). Ovary on gynophore ..... Subgenus *Afroswartziani* section *Microdendron* (Africa)

32. Branchlets and flowers not purplish; stamens 3, filaments mostly free or united to 2/3 of length; pollen 4-colporate, exine (hetero-)reticulate; pistillate sepals 5; pistillate disc entire; stigmas free, bifid, tips sometimes subcapitate 33
32. Branchlets and flowers often purplish; stamens 2 or 3, filaments connate; pollen pantoporate, exine shields elongated or if round with only 1 pila; pistillate sepals 6; pistillate disc dissected or lobed; stigmas free or connate, bifid to emarginate, tips not capitate ..... 34 (Subgenus *Cyclanthera*)

33. Anther connective not enlarged, thecae not stipitate; style branches sub-

capitate; seeds verrucate ..... Subgenus *Phyllanthus* section *Phyllanthus* subsection *Niruri* (South America, pantropically invasive)

33. Anther connective variable, deeply emarginate with the two thecae appearing stipitate; style branches not capitate; seeds striate or linearly verrucate..... .....Subgenus *Phyllanthus* section *Phyllanthus* subsection *Clausseniani* (South America)

34. Branchlets unramified, rooting at nodes; leaves crisply succulent; stamens 2, filaments free; pollen shields elongated (banded) (Webster & Carpenter 2002) .....Subgenus *Cyclanthera* section *Callitrichoides* (West Indies)

34. Branchlets often with 1 or 2 lateral branches (bipinnatiform), not rooting at nodes; leaves not succulent; stamens 3, filaments completely connate into a circular synandrium; pollen shields isodiametric, each with a central pila surrounded by a murus (Webster & Carpenter 2002) ..... Subgenus *Cyclanthera* section *Cylcanthera* (West Indies)

35. Stamens 3, filaments free, anthers dehiscing horizontally; pistillate disc dissected; pollen grains brevicolporate and diorate or porate, exine pilate; seeds verruculose ..... Subgenus *Conami* section *Apolepsis* (South America)

35. Stamens 2 or 3, filaments entirely or partially connate (free in *P. warnockii* G.L.Webster), anthers dehiscing oblique to horizontally (vertically in *P. warnockii*); pistillate disc entire; pollen 3-colporate, exine reticulate; seeds smooth or longitudinally striate..... Subgenus *Swartziani* (North America, pantropical invasive)

36. Leaves reduced and branchlets transformed to phylloclades (at least in older branches) 37

36. Leaves not reduced and branchlets not transformed to phylloclades..... 39

37. All stems rounded or flat; stipules unilaterally auriculate, stamens free or connate; pollen 3–4-colporate, exine reticulate ....38 (Subgenus *Phyllanthus* section *Choretropsis*)

37. Lateral stems flattened with wide phylloclades, (bi-)pinnatiform; stipules not auriculate; stamens usually united at base; pollen clypeate, exine areolate..... ..... Subgenus *Xylophylla* section *Xylophylla* (West Indies)

38. Main axes often flat, branching monopodial, leaves distichous; inflorescences usually bisexual, stamens 3 (rarely 4)..... Subgenus *Phyllanthus* section *Choretropsis* subsection *Applanata* (South America)

38. Main axes rounded, branching monopodial or sympodial, leaves spiral; inflorescences mostly unisexual; stamens 2 or 3.....

....Subgenus *Phyllanthus* section *Choretropsi*s subsection *Choretropsis* (South America)

39. Fruits indehiscent, berries or drupes..... 40
39. Fruits dehiscent, capsules (or absent)..... 48

40. Fruits drupaceous..... 41
40. Fruits baccate..... 43

41. Sepals 6; stamens 3, filaments connate.....Subgenus *Emblica* section *Emblica* (Asia)
41. Sepals 4–6; stamens 3–4(rarely 2 or 5), filaments free ..... 42 (Subgenus *Kirganelia* section *Cicca*)

42. Plants dioecious; disc absent in both sexes; staminodes absent; fruits spongy (Webster 1957) .... Subgenus *Kirganelia* section *Cicca* subsection *Aporosella* (West Indies and South America)
42. Plants monoecious; disc present in both sexes; sometimes staminodes present; fruits hard..... .....Subgenus *Kirganelia* section *Cicca* subsection *Cheramella* (commonly cultivated, origin possibly African?)

43. Stamen 2, filaments connate; ovary 2-locular ....Subgenus *Kirganelia* section *Chorisandra* (Africa, Madagascar, Mainland Asia)
43. Stamen 3–6, filaments free or connate; ovary 3-locular..... 44

44. Branchlets subtended by reduced leaves, but not cataphylls, flowers on brachyblasts; stamens 3, filaments free or connate..... .....Subgenus *Conami* section *Hylaeanthus* (South America)
44. Branchlets subtended by (spinescent) cataphylls, stamens 4–6, filaments free. 45

45. Branchlets subtended by spinescent cataphylls; stamens 5 in 2 sets, one free and the other basally fused ....Subgenus *Kirganelia* section *Anisonema* (Africa and Asia)
45. Branchlets subtended by scale or stipule like cataphylls; stamens 4–6, filaments free 46

46. Staminate inflorescences on separate (leafless) plagiotropic branches, pistillate flowers axillary — seeds globular, smooth..... Subgenus *Kirganelia*

section *Polyanthi* (Africa)

46. Inflorescences axillary, on all plagiotropic branches 47

47. Stamens 5 ..... Subgenus *Kirganelia* section *Hemicicca* (Asia)
47. Stamens 6 ..... Subgenus *Kirganelia* section *Chorisandra* (Africa, Madagascar, Mainland Asia)

48. Anthers apiculate..... 49
48. Anthers non-apiculate 56

49. Sepals often caudate-acuminate; filaments connate, staminate disc consisting of linear spathulate segments; pistillate disc entire — pollen 4-colporate, exine reticulate.....50 (Subgenus *Phyllanthodendron* (Asia)
49. Sepals often acuminate, but not caudate; filaments free or connate, staminate disc segmented, globular; pistillate disc entire (or absent)..... 54

50. Shoots not differentiated, all leaves similar in size, flowers on lateral shoots51
50. Shoots differentiated into sterile leaf bearing shoots with larger leaves and fertile shoots with smaller leaves..... 53

51. Sepals 4 in staminate flowers; stamens 4; pistillode present..... Subgenus *Phyllanthodendron* section *Tetrandrum* (Asia)
51. Sepals 5–6 in staminate flowers; stamens 3; pistillode absent..... 52

52. Shrubs; sepals 5 in staminate flowers. Fruit reminiscent of *Actephila* (Croizat 1942a) ..... Subgenus *Phyllanthodendron* section *Pseudoactephila* (Asia)
52. Twining shrubs; Sepals 6 sepals in staminate flowers .... Subgenus *Phyllanthodendron* section *Arachnodes* (Asia)

53. Trunk often succulent and enlarged at base; leaf blades >6 cm long .... Subgenus *Phyllanthodendron* section *Phyllanthodendron* (Asia)
53. Trunk not succulent or enlarged at base; leaf blades <6 cm long .... Subgenus *Phyllanthodendron* section *Calophyllum* (Asia)

54. Filaments connate .Subgenus *Xylophylla* section *Ciccastrum* (South America)
54. Filaments free 55

55. Leaves with or without laminar glands; sepals in two indistinct whorls; pollen 4–8-colporate or diorate.... Subgenus *Emblica* section *Microglochidion* (South America)
55. Leaves without laminar glands; sepals in two distinct whorls; pollen 3-syncolporate .....67 (Subgenus *Gomphidium*)

56. Leaves opposite or subopposite 57
56. Leaves alternate 59

57. Bark lenticellate; filaments connate ....Subgenus *Xylophylla* section *Williamia* subsection *Mirifici* (Cuba)
57. Bark smooth; filaments free 58

58. Branchlets sometimes opposite bipinnatiform; staminate sepals 5, not distinctly biseriate; staminate disc consisting of 5 free segments; stamens 5.... .....Subgenus *Menarda* (Madagascar and Middle East(?))
58. Branchlets pinnatiform, not opposite; staminate sepals 5 or 6, in both sexes often distinctly biseriate; staminate disc entire, 3 emarginate segments or 5–6 massive segments; stamens mostly 3 or 5 (up to 20)..... 67 (Subgenus *Gomphidiumn*)

59. Sepals 4 in staminate flowers; stamen 2, filaments connate— pollen pantoporate or clypeate 60
59. Sepals 5 or 6 in staminate flowers; stamens 3–15, filaments free or connate66

60. Leaf margins very thick, conspicuously revolute; staminate disc massive, entire; pollen clypeate.....Subgenus *Xylophylla* section *Glyptothamnus* (Cuba)
60. Leaves margins not thickened, sometimes slightly revolute; staminate disc segmented; pollen pantoporate or clypeate. 61

61. Anthers dehiscing vertically; sepal margins entire 62
61. Anthers dehiscing horizontally/transversely; sepal margins entire to dentate or lacerate 64

62. Inflorescences usually bisexual, appearing with the expanding leaves (Webster 1958); pollen clypeate; style connate in a tube and stigmas often reduced to acute tipsSubgenus *Xylophylla* section *Thamnocharis* (West Indies)
62. Inflorescences mostly unisexual, appearing after the leaves; pollen pantoporate; style connate or free 63

63. Ovary papillose or verrucullose, 3-locular ..... Subgenus *Eriococcus* section *Eriococcodes* (Asia)
63. Ovary smooth, 6-locular... Subgenus *Eriococcus* section *Nymphanthus* (Asia)

64*. Stigmas entire, connate. Filaments thickened at top .... Subgenus *Eriococcus* section *Emblicastrum* (Asia to Australia)
64*. Stigmas entire or emarginate....Subgenus *Eriococcus* section *Scepasma* (Asia)

64*. Stigmas free, bifid ..... 65 (Subgenus *Eriococcus* section *Eriococcus*)

65. Flowers in all leaf axils ..... Subgenus *Eriococcus* section *Eriococcus* (Asia)
65. Pistillate flowers on leafy panicles at end of branchlets and staminate flowers closer to the base of branchlets without leaves (see Brunel 1987) ..... Subgenus *Eriococcus* section *Eriococcus* subsection *Spiciferens* (Asia)

66. Branchlets (bi-)pinnatiform; sepals often biseriate; staminate nectar disc often 3 massive emarginate (or 6 separate) segments to absent, stamens may be inserted on a wide receptaculum — pollen 3–(syn-)colporate ..... 67 (Subgenus *Gomphidium*)
66. Branchlets pinnatiform; sepal whorls indistinct; staminate nectar disc entire or segmented 79

67. Branchlets bipinnatiform 68
67. Branchlets pinnatiform 70

68. Axes incrustate or hirsutulous with red hairs; stamens 2–6; pollen clypeate ..... Subgenus *Xylophylla* section *Hemiphyllanthus* (West Indies)
68. Axes not incrustate or hirsutulous, hairs usually white; stamens mainly 3–5 (up to 20); pollen 3-(syn)colporate 69

69. Inflorescences glomerules; pollen diverse, often 3-colporate or porate with diorate colpi (see Webster & Carpenter 2002), exine vermiculate to pilate. Fruit conspicuously veined ..... Subgenus *Conami* section *Nothoclema* (South America)
69. Inflorescences glomerules or panicles; pollen 3–4-syncolporate with vermiculate/rugulate exine (Lobreau-Callen et al. 2011); fruit smooth ..... Subgenus *Gomphidium* section *Nymania* (Southeast Asia, mostly New Guinea)

70. Disc absent or rudimentary in both sexes 71
70. Disc entire or segmented in both sexes 74

71. Sepals 6, biseriate, inner whorl petal-like, pistillate sepals leafy; stamens 3; ovary 3-locular. Calyx in fruit saccate ..... Subgenus *Gomphidium* section *Gomphidium* subsection *Physoglochidion* (New Caledonia)
71. Sepals 5–6, not distincly biseriate; stamens(3–)5(–15), ovary 3–5-locular .. 72

72. Sepals 5; stamens 5; ovary 4–5-locular ..... Subgenus *Gomphidium* section *Leptonema* (New Caledonia)
72. Sepals 5 sometimes 6; stamens mostly (3–)5(– 15); ovary 3-locular 73

73. Disc rudimentary in both sexes; filaments shorter than anthers, inserted on a wide receptaculum ..... Subgenus *Gomphidium* section *Adenoglochidion* (Southeast Asia, New Caledonia)
73. Disc rudimentary or absent in both sexes; filaments longer than anthers, diverging from center of receptaculum ..... Subgenus *Gomphidium* section *Adenoglochidion* subsection *Eleutherogynium* (New Caledonia)

74. Stamens connate 75
74. Stamens free 76

75. Inflorescences glomerules; pollen diverse, often 3-colporate or porate with diorate colpi (see Webster & Carpenter 2002), exine vermiculate to pilate; fruit conspicuously veined ..... Subgenus *Conami* section *Nothoclema* (South America)
75. Inflorescences glomerules or paniculate; pollen 3–4-syncolporate, exine vermiculate/rugulate (Lobreau-Callen et al. 2011); fruit smooth ..... Subgenus *Gomphidium* section *Nymania* (Southeast Asia, mainly New Guinea)

76. Sepals 5, not distinctly biseriate; stamens mostly (3–)5(–15), filaments free; disc consisting of 3 emarginate segments or absent ..... Subgenus *Gomphidium* section *Adenoglochidion* (Southeast Asia New Caledonia)
76. Sepals 5 or 6, often biseriate (except in *P. tuerckheimii* G.L.Webster); stamens 3, filaments free or connate; disc of consisting of 3 emarginate segments or 6 free segments 77

77. Sepals 5; pollen grains not syncolpate, colpi without distinct borders; exine reticulate ..... Subgenus *Gomphidium* section *Calodictyon* (South America)
77. Sepals 6; pollen grains with marginate colpi, often meeting at poles; exine reticulate or ± vermiculate 78

78*. Inflorescences axillary cymules; pollen 3-syncolporate with fine to course reticulate exine ..... Subgenus *Gomphidium* section *Gomphidium* (Southeast Asia, New Caledonia)
78*. Inflorescences glomerules or panicles; pollen 3-syncolporate with vermiculate/rugulate exine ..... Subgenus *Gomphidium* section *Nymania* (Southeast Asia, mostly New Guinea)
78*. Inflorescences glomerules; pollen diverse, often 3-colporate with diorate

colpi (see Webster & Carpenter 2002), exine vermiculate to pilate. Fruit conspicuously veined..... .....Subgenus *Conami* section *Nothoclema* (South America)

79. Staminate disc entire..... Subgenus *Xylophylla* section *Adianthoides* (South America)
79. Staminate disc segmented..... 80

80. Filaments free or only fused at base..... 81
80. Filaments fused at least partially to completely, sometimes fused in separate sets or whorls..... 89

81. Leaves often with glands; anthers apiculate. Leaves thick; style entire .... Subgenus *Emblica* section *Microglochidion* (South America)
81. Leaves without glands; anthers not apiculate..... 82

82. Stamens 3 83
82. Stamens 4 or 5..... 85

83. Brachyblasts often present; inflorescences cauliflorous; sepals 6..... .....Subgenus *Kirganelia* section *Ciccopsis* (South America)
83. Brachyblasts absent; inflorescences axillary; sepals 5..... 84

84. Leaf blades <8 cm long; anther connective enlarged; pollen 4-colporate..... Subgenus *Phyllanthus* section *Phyllanthus* subsection *Clausseniani* (South Ameria)
84. Leaf blades >8 cm long; anther connectives not enlarged; pollen perisyncolporate — Pistillate pedicel quite massive (up to 3 cm wide (Brunel 1987)), fruit ornamented..... ..... Subgenus *Ceramanthus* section *Ebolowani* (Africa)

85. Pistillate sepals 8–10 .... Subgenus *Xylophylla* section *Diplocicca* (South America)
85. Pistillate sepals 5 or 6..... 86

86. Brachyblasts present 87
86. Brachyblasts absent..... 88

87. Inflorescences (stalked) fascicles; stamens 5, filaments completely free; fruits 3-locular, dehiscent; seeds kidney-shaped, smooth with mottled patterns (similar to seeds of *P. juglandifolius* Willd.)..... .....Subgenus *Kirganelia* section *Omphacodopsis* (Africa)

87. Inflorescences panicles; stamens 4 or 5, filaments free or sometimes basally fused; fruits 3–5-locular, indehiscent; seeds globular, smooth ..... Subgenus *Kirganelia* section *Polyanthi* (Africa)

88. Stamens 3–5, free or slightly fused at base; anthers dehiscing vertically; fruits capsular; seeds smooth or faintly longitudinally striate..... Subgenus *Anesonemoides* (Africa, Madagascar, Asia)
88. Stamen 2–5(–7); anthers dehiscing horizontally; fruits capsular; seeds smooth .....Subgenus *Emblica* section *Pityrocladus* (South America)

89. Stamens fused in several whorls or sets 90
89. Stamens fused in a central column 93

90. Brachyblasts present; stamens fused in two sets with one central column and two separate free stamens 91
90. Brachyblasts absent; stamens in 2 or 3 whorls, fused in various ways..... 94 (Subgenus *Xylophylla* section *Willamia* (West Indies)

91. Pollen 3-colporate, exine pilate or reticulate 92
91. Pollen clypeate, exine areolate .....94 (Subgenus *Xylophylla* section *Willamia,* West Indies)

92. Exine pilate.....Subgenus *Kirganelia* section *Brazzeani* (Africa)
92. Exine reticulate..... Subgenus *Kirganelia* section *Anisonema* (Africa and Asia)

93. Stems and branchlets incrustate with dark platelets of bark or lenticellate.. 94
93. Stems smooth..... 95

94*. Stems smooth; leaves alternate; stamens 3–15 in 3 whorls, connate in various ways; stigmas erect but not lacerate. Sepals 5 or 6..... ...Subgenus *Xylophylla* section *Williamia* subsection *Discolores* (West Indies)
94*. Stems and branchlets incrustate with small dark platelets on the fissured bark; leaves alternate; stamens (2)3–6 with filaments connate, usually in 2 whorls; stigmas erect, conspicuously lacerate (see Webster 1958)..... ....Subgenus *Xylophylla* section *Williamia* subsection *Incrustati* (West Indies)
94*. Stems smooth but prominently lenticellate; leaves opposite; stamens 5 with filaments connate, but 2 anthers inserted lower than the other 3; stigmas reflexed and covering the ovary, apex sometimes blunt ....Subgenus *Xylophylla* section *Williamia* subsection *Mirifici* (West Indies)

95. Pollen 3–5-colporate or 5-brevicolporate (Webster & Carpenter 2008), exine reticulate, microperforate or scabrous (Africa and Asia) 96

95. Pollen clypeate, exine areolate (Americas) .....99 (Subgenus *Xylophylla*)

96. Anthers dehiscing obliquely to horizontally; exine microperforate or scabrous..... Subgenus *Afroswartziani* (pantropical, mostly African)
96. Anthers dehiscing vertically; exine reticulate .....97 (Subgenus *Emblica*)

97. Sepals mostly 5; staminate disc consisting of 5 segments; stamens 2–5(–7); anthers dehiscing horizontally; pollen 3–5-colporate; pistillate disc entire or segmented .....Subgenus *Emblica* section *Pityrocladus* (South America)
97. Sepals 6; staminate disc consisting of 6 segments; stamens 3; anthers dehiscing vertically; pollen 4–5-colporate or 5-brevisulcate; pistillate disc entire 98

98. Inflorescences appearing paniclulate in leaf axils; pollen 5-brevisulcate..... .....Subgenus *Emblica* section *Botryoides* (Asia)
98. Inflorescences found along entire branchlet as axillary cymules; pollen 4–5-colporate..... Subgenus *Emblica* section *Emblica* (Asia)

99. Inflorescences cauliflorous thyrses; stigmas petaloid..... .....Subgenus *Xylophylla* section *Epistylium* (West Indies)
99. Inflorescences axillary cymules; stigmas tapering, not petaloid, sometimes fused into a tube 100

100. Leaf blades mostly 1–2 cm long, with mesophyllar sclereids; stamens 3–7..... .....Subgenus *Xylophylla* section *Orbicularia* (West Indies)
100. Leaf blades >2 cm long, sometimes with mesophyllar sclereids; stamens 2–7(–8) 101

101. Brachyblasts often present; sepals 5; staminate disc consisting of 5 segments; stamens 3 (rarely 4); fruit a large fleshy capsule (usually >2 cm in diameter).. .....Subgenus *Xylophylla* section *Omphacodes* (West Indies)
101. Brachyblasts absent; sepals 4–6; staminate disc usually consisting of 6 segments; stamens 2–7(–8); fruit small dry capsule (<1 cm in diameter) . 102

102. Staminate sepals 5, pistillate sepals 6; inflorescences mostly unisexual cymules appearing after the leaves, several pistillate flowers per node; stamens 3–7, thecae dehiscing horizontally; style present, elongated and exerted from calyx, stigmas dilated, bifid to multifid..... .....Subgenus *Xylophylla* section *Oxalistylis* (South America)
102. Sepals in both sexes 4–6; inflorescences bisexual cymules appearing with the expanding leaves on new branchlets, usually only 1 or 2 pistillate flowers among several staminate flowers; stamens 2–6 (or 8), thecae dehiscing

vertically; style like an erect tube, stigma branches narrowed to acute tips.....
Subgenus *Xylophylla* section *Thamnocharis* (West Indies)

Discussion & Conclusion

Taxonomic discussions on the circumscription of genus *Phyllanthus* are still ongoing, mainly with the question whether the genera nested within should be subsumed (Hoffmann et al. 2006) or remain separate (van Welzen et al. 2014a). However, a good understanding and clear structure within the genus *Phyllanthus* in its current circumscription is necessary. Here an attempt was made to summarize over 200 years of taxonomic work on this immense group. Several issues that still exist will hopefully be resolved in new systematic studies. The provisional key to the subgenera and (sub) sections provided here works with most typical examples of *Phyllanthus* species. Future research and revision work should focus on treatments of the individual subgenera and/or sections within the genus.

Unfortunately not all species could be fitted in this subgeneric classification due to exceptional characters or incomplete descriptions (see Appendix 3-2). These will need further study or more new collections to elucidate their place within the genus. Often these are species of which only the type specimen is known and which were not collected since, and some might be extinct (e.g., *P. aoraiensis* Nadeaud; Wagner & Lorence 2011), or they might be exceptional forms, which should be united with other species. For some we could only assign them to subgenus level and further revision work should place them in their appropriate sections. The placement of some species may change with new research and we welcome these changes as they will lead to a better understanding of the genus *Phyllanthus* and we hope this article inspires discussion.

Several issues are still unresolved and will require further attention. Subgenus *Phyllanthus*, which previously spanned all herbaceous species, remains difficult and more species need to be included in new phylogenetic studies. Several groups in our list have not had formal taxonomic treatment for some time and new revision work may identify new species and better characters to differentiate them within *Phyllanthus*. Another taxonomic problem was created by the discussions on the validity of Brunel's thesis (1987), which has led to many species being published twice under different names (see Radcliffe-Smith 1996b). This will require close scrutiny in determining how many should be synonymized. Finally, a decision should be made on how to treat the paraphyly of the genus *Phyllanthus*. Whether the genus will be split or whether the clades will be subsumed within *Phyllanthus*, we hope that this treatment will provide structure to this diverse genus.

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Appendix 3-1. Synopsis of the infrageneric classification of the genus *Phyllanthus*. Author of type species can be found in Appendix 3-2. Countries in parentheses indicate unlikely disjunct ditributions that require further study. Available at: https://doi.org/10.3767/blumea.2018.63.02.14

Appendix 3-2. Species checklist of *Phyllanthus* based on the current infrageneric classification. Each species denotation contains information on whether the classification was based on morphology, literature references or phylogenetic evidence. Unsure placements are noted with 'loc' for location based placements, a question mark and/or a ~ symbol when morphology does not completely comply with the group. Available at: https://doi.org/10.3767/blumea.2018.63.02.14